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THIGMOTACTIC REACTIONS OF THE FRESH WATER TURBELLARIAN, *PHAGOCATA GRACILIS*, LEIDY

BY

BERNOL R. WEIMER

The Turbellaria have ever been popular subjects for experimentation, yet in looking over the literature, I find that very little has been done upon the thigmotactic reactions of these animals. Thinking that here was a problem that might yield some interesting results, I collected a number of the animals in Falling Run, Morgantown, West Virginia, and these were used in the following experiments. Five specimens were sent to Dr. H. S. Pratt of Haverford College, and were identified by him as Phagocata gracilis.

Six rocks of varying degrees of roughness were collected and cemented together with Portland cement in a circular glass dish 7 cm. high. The rocks were so arranged as to form a surface as nearly flat as possible. The outer walls of the dish were covered with heavy black paper in order that light could fall only vertically upon the surface of the rocks.

After allowing water, which was changed frequently, to stand in the dish for three weeks, some animals were placed in the dish. All the animals were in good condition, but those animals which came in contact with the cement between the rocks, secreted a slimy substance and died. The cement was then coated with paraffin, and at the same time a piece of glass of nearly the same area as the different rock surfaces, was waxed in.

After carefully washing the paraffin for two days in running water, some animals were again placed in the dish and after two days were alive and in good condition. Forty animals were then put into the dish which was placed beneath the skylight in a room so darkened that all the light came from this source. The surface of the rocks in the experiments was covered by water to an average depth of 1.5 cm. The temperature of the water varied from 21° -25° C.

In collecting the rocks used in the experiments, care was taken that the surface should have different degrees of roughness and that each rough surface should be as nearly uniform as possible. The rocks and the glass plate were each numbered with India ink. These numbers are used in the tables given, to designate the rock and, obviously, the surface. Rocks numbered 1, 2, 3, and 4 were of weathered sandstone and rock number 5 of weathered lime-stone.

The surface of rock number one was composed of rounded quartz crystals of about the same coarseness as granulated sugar. Rock number two had a surface somewhat smoother than number one, the particles of sand were about as coarse as table salt. Rocks numbered four, three and six approached, in the order mentioned, rock number five, a smooth lime stone. Thus the rock surfaces varied in coarseness or roughness of surface from particles the size of granulated sugar to a comparatively smooth surface in the following order: one, two, four, three, six, and five. For a surface a grade smoother than the rocks described, there was the glass plate and the paraffin coating the cement. Practically the only surface difference noticed between the glass and the paraffin was, that the paraffin had a slightly greasy feeling.

The following explanation refers to tables 1 and 2. The total number of animals counted on a given surface during a set of observations was found and this number, divided by the number ofobservations in the set, gave the average observation for the set. This average observation for each set was added and the average of this total gave the average observation for all the sets. Since only one set of observations was taken in tables 3 and 4, the second average of the sets, was not necessary. The area of the paraffin and the vertical glass sides of the dish covered by water were averaged as one surface (para-glass in tables). This para-glass surface was used as the common unit area and from this the relative number of animals resting on a common unit surface, was computed. Since the paraffin and the vertical glass surface was so nearly alike, both were averaged as one. With this brief explanation, the tables given should not be difficult to understand.

The data set forth in table 1 was procured in the following way. The observations were taken at either ten or fifteen minute intervals and usually after each observation the animals were stimulated, i.e. caused to move from the place they were resting. No distinction was made between an animal moving across and one at rest on a surface. This probably accounts for the high averages for the various surfaces in table 1. The dish was frequently moved around to counteract any light reaction, tho the light apparently made no difference since it came vertically from above. A tendency to gather in groups was also noticed. These groups were usually found on the paraffin. The animals in these groups were always stimulated after an observation.

TABLE 1

No. of lbs.	10	10	8	10	8	7	15	Total 68		
	av. set1	av. set2	av. set3	av. set4	av. set5	av. set6	av. set7	av. of all obs.	No. animals per unit surface	Total no. of animals counted
Rock										
1	1.70	1.80	2.75	0.70	2.00	4.30	1.60	2.13	25.53	145
2	2.40	1.20	1.50	0.40	2.55	3.66	0.46	1.73	15.65	108
3	2.10	3.40	2.70	1.10	2.44	2.50	1.05	2.19	18.79	249
4	0.90	4.80	8.25	0.50	2.20	1.16	1.90	2.81	34.59	192
5	2.30	2.40	1.66	0.80	1.60	2.30	1.90	1.85	15.17	126
6	1.40	1.20	1.40	1.30	1.70	3.60	1.26	1.66	17.66	113
Glass 7	1.70	0.90	1.00	0.70	1.30	2.10	1.20	1.27	16.25	86
Para-glass	32.70	28.50	25.12	34.50	28.30	30.30	31.86	30.18	30.18	2053

Observations showing number of animals seen on each surface with vertical illumination only. The time between sets varied from a day to a week. The surfaces in order from roughest to smoothest are as follows: one, two, four, three, six, five and glass.

From table 1 it is seen that when all the surfaces have been reduced to the same unit area, the three highest averages of animals resting, are as follows, rock four, 34.59, paraffin-glass, 30.18 and rock one 25.53. The other surfaces have much lower averages and do not vary much among themselves. One peculiar fact to be noticed is that rock one has the roughest surface, the glass-paraffin has the smoothest surface, and intermediate between these two is the surface of rock four. It would be well to remember that after each observation the animals were stimulated. Since so few animals were found resting, they were averaged with those moving.

The data in table 2 differs from that found in table 1, in that all the observations were taken in a photographic dark room. An electric light was used only long enough to record the observation. The observations were taken at intervals varying from 30 minutes to an hour and the animals moved from their resting position after each observation. As a result of the longer interval elapsing, most of the animals were found resting when the observation was recorded.

TABLE 2

No. of obs.	4	6	6	4	Total 20		
	av. set 1	av. set 2	av. set 3	av. set 4	av. of all obs.	No. of animals per unit surface	Total no. of animals counted
Rock 1	0.00	1.50	1.60	0.75	.96	11.41	192
2	2.00	3.00	1.16	0.25	1.60	14.38	32.00
3	1.00	2.33	0.80	2.50	1.65	14.15	33.00
4	1.50	1.50	0.16	1.00	1.04	12.80	21.00
5	0.25	1.66	6.10	1.00	2.22	18.20	45.00
6	1.50	0.50	3.00	3.75	2.18	23.06	44.00
Glass 7	1.50	2.30	1.50	0.25	1.38	17.66	28.00
Para-glass	32.75	25.60	27.60	30.75	29.17	29.17	584

Observations taken in photographic dark room showing number of animals counted on each surface. The time between sets varied from a day to a week.

The surfaces in order from roughest to smoothest are as follows: one, two, four, three, six, five and glass.

The averages of these observations in table 2 show, that when all the surfaces have been reduced to the same unit area, the surfaces having the most animals resting upon them are the paraffin-glass, 29.17, and rock six, 23.06. Rock six has a comparatively smooth surface of weathered lime-stone. The averages for the other surfaces are about the same.

After conducting the first set of experiments, the results of which are found in tables 1 and 2, the glass was broken from around the cement block containing the rocks. The cement necessarily exposed was covered with a coating of bees wax. The whole block, surface downward, was then placed upon three glass supports, 2.5 centimeters high, in an enameled pan. The pan was then filled with water until it covered the surface of the rocks. This apparatus was first put in a photographic dark room, and observations taken each hour by lifting the rocks. The results were so decidedly negative that only a few observations were taken. See table 3. The animals not only did not rest upon the rock surfaces but were found scattered in average numbers over the entire bottom and sides of the pan. Only an average number was found on the bottom of the pan underneath the rocks.

TABLE 3

Surface	Observations					Av.	No. animals per unit surface	Total no. animals counted
Rock 1						Av.		
2	1					0.20	1.19	1
3		2				0.40	3.43	2
4								
5								
6								
Glass								
Para.								
Pan	39	38	40	40	40	39.90	39.90	237

One set of five observations taken in photographic dark room with the rocks inverted, showing the number of animals counted on each surface.

The surfaces in order from roughest to smoothest are as follows: one, two, four, three, six, five and glass.

TABLE 4

Surface	Observations									Av.	No. animal per unit surface	Total no. animals counted
Rock 1												
2									1	0.09	0.80	1
3												
4												
5									1	0.09	0.73	1
6												
Glass												
Para.					1		1			0.18	0.18	2
Pan	40	40	40	40	39	40	39	40	38	39.5	39.50	435

One set of nine observations taken with vertical illumination only and with rocks inverted, showing the number of animals counted on each surface.

The surfaces in order from roughest to smoothest are as follows: one, two, four, three, six, five and glass.

The same apparatus was then placed underneath the skylight in a room so darkened that all the light came from this source. The same negative results were obtained as in the photographic dark room, though the difference was noted in that the animals in this experiment, gathered on the pan underneath the rocks, whereas in the dark room this preference was not shown.

According to Pearl ('02), the ventral surface of Planaria maculata is strongly positively thigmotactic; but this does not explain the tendency of the animals to rest in angles. This resting in angles he calls goniotaxis. The physiological condition of reduced tonus helps to determine whether or not the animal will rest on a smooth surface.

The increased resistance to movement may be one cause for stopping on the uneven surface tho the most important factor is probably light. Nevertheless, instances are known where the animal may stop in a bright light, tho such instances are rare.

From table 1 it is seen that rock four has an average of 34.59 animals per unit area. The surface of this rock in degree of roughness, is midway between the rough granular surface of rock number one (average 25.53) and paraffin-glass (average 30.18). Table 2 shows that the paraffin-glass surface (average 29.17) is the highest per unit area, followed by rock six (average 23.06) whose surface is of smooth weathered limestone. In tables 1 and 2, it will be noticed that surface number seven is of glass. This surface is horizontal, not vertical as is that averaged with the paraffin. If the average of this surface (16.25 in table 1 and 17.66 in table 2) were added to the surface average of the paraffin-glass (average 30.18 in table 1 and 29.17 in table 2), the total average of these surfaces would be 46.43 in table 1 and 46.83 in table 2. This is much higher than any of the rough surfaces. From this the conclusion may be drawn that the animals prefer a smooth surface.

Pearl ('02), in describing the method of locomotion of Planaria maculata says that the ventral surface of the body constantly secretes mucus in greater and lesser quanities. This is very sticky and under normal conditions adheres to the surface on which the animal reposes. Thus between the animal and the surface on which it moves there will be a constant layer of mucus. The beating of cilia in this mucus pushes the animal forward. Considering this explanation, then, more mucus may be secreted by an animal when passing over a rough surface than when passing over one that is smooth. Likewise a regular granular surface might not have quite so much effect as a very angular surface. Pearl ('02), also suggests that the reduced physiological tonus of the animal might cause it to rest on the rough surface.

To find whether or not more mucus was extruded and secreted when passing over a rough surface than over a smooth one, the following experiment was tried. A piece of ordinary window glass was scratched or grooved by a diamond glass cutter. The glass with the grooved surface was then placed in a large petri dish and covered with water. Some of the animals were then placed in the dish and allowed to move over the grooved surface. After an hour the animals were removed and the glass "developed" by immersing in Delafields' hematoxylin, which stained the slime blue. This gave better results than the method used by Pearl ('02), who used a solution of carmine. This was tried and the carmine particles by adhering to the mucus, showed the tracks but the mucus was not stained and hence a close study of it could not be made. The glass was then broken so that cross sections of the grooves could be examined with the microscope. A number of sections were thus examined but at no place could a greater slime secretion be noticed where the slime tracks crossed a groove.

Thinking perhaps that the width and depth of the grooves in a surface might cause some difference in the amount of slime secreted, the bottom of a large petri dish was covered by a layer of paraffin to an average depth of 5 mm. In this paraffin were cut grooves varying from 0.20 to 3 mm. in width and the same in depth. The dish was then filled with water and in it were placed some animals. The smaller grooves did not seem to reduce the rate of locomotion of the animals. However, when an animal approached one of the wider grooves, it would hesitate, raise up the anterior end of the body and move it to and fro, then pass across without touching the bottom of the groove.

After the animals had been undisturbed for two hours, they were removed and the water replaced by a solution of Delafields' hematoxylin. On examination of the stained slime tracks it was found that in few cases was there a greater amount of slime secreted. The slime strands did not descend to the bottom of the grooves but in most cases were continued on across as a sort of bridge. In some cases these strands were broken but even then no abnormal amount of slime was found. At the edges of the grooves, however, there were places where there seemed to be a greater amount of slime. These were the places, probably, where the animals hesitated.

From these results it would appear that there is the same amount of slime on all surfaces and that no abnormal secretion is caused by a rough surface. Thus a change in the physiological condition of the animal as caused by the difference in mucus secretion, would not effect the thigmotactic reaction to surfaces of varying roughness and smoothness.

Pearl ('02), suggests that perhaps the rough surface offers more resistance to movement than does a smooth surface. This naturally would cause a slower rate of locomotion when an animal was passing over a rough than when passing over a smooth surface but since an equal amount of slime is secreted on all surfaces, there should be approximately the same rate for all surfaces. Accordingly the rate of locomotion was found for two surfaces, the one of rough sandstone, somewhat coarser than rock one, and the other glass.

A piece of white paper was marked off in 1 cm. squares and placed underneath a large petri dish filled with water. The surface of the rock was marked off in 1 cm. squares with waterproof India ink and around the edges were placed sides of pasteboard to keep the animals from wandering off the surface. The rock was placed in a galvanized pan which was filled with water to such a height that the surface of the rock was covered to a depth of 2 cm. The two surfaces were placed underneath the skylight in a room from which all other sources of light were cut off.

The four animals used in these experiments were kept in separate dishes carefully marked. When the animals were transferred from these dishes to the surfaces, a camel's hair brush was used in order not to injure them. In the course of these experiments, animal number one died, so that most of the tables show the results of the reactions of numbers two, three and four, all of which were active, healthy, individuals. The animals were placed on the surface singly, and a number of observations taken by means of a stop watch, as to the length of time required to move over 1 cm. of surface. No allowance was made for an approximate deviation of 2 mm. from a straight line in passing over 1 cm. of surface.

The data recorded in table 5 was procured thus. A number of observations of the rate of locomotion of each animal was taken on two consecutive days for the glass surface and on the two following days for the rock.

TABLE 5

Animal	Rock 1st day		Rock 2nd day		Av. rate in mm. per sec.	Glass 1st day		Glass 2nd day		Av. rate in mm. per sec.
	no. of obs.	av. rate in mm.	no. of obs.	av. rate in mm.		no. of obs.	av. rate in mm.	no. of obs.	av. rate in mm.	
1	15	0.92	15	1.23	1.07	10	0.74			0.74
2	15	0.80	15	1.10	0.95	16	1.43	18	1.2	1.31
3	15	1.05	15	1.17	1.11	17	1.47	18	1.46	1.46
4	15	0.97	15	1.24	1.10	18	1.38	18	1.47	1.42

Observations showing the rate of locomotion. Observations taken on one surface only each day

Table 5 shows that the average rates per second of animals number three and four are the highest, being 1.11 mm. and 1.1 mm. on the rock and 1.46 mm. and 1.42 mm. on glass. This shows a difference in rate of speed per second between the glass and the rock of 0.35 mm. and 0.32 mm. Animal number two shows a difference per second of .36 mm. In these three instances the animals moved more rapidly on the glass. However, a further examination shows that an animal in twenty-four hours time will vary in rate of locomotion on the rough surface .31 mm. and on the smooth .21 mm. per second. Walter ('02), who tested the rate of speed on glass only, found that the rate varied from 1.22 mm. to .96 per second. So the variation in rate between the two surfaces can scarcely be attributed wholly if at all, to the difference between the two surfaces but to some other factor. This is further proven by a study of tables 6 and 7.

The data in tables 6 and 7 differs from that in table 5 somewhat. A number of observations on the rate of locomotion of an animal was taken first on one surface and immediately on the other. Several hours later another set of observations was taken. This lessened the chance for so great a change physiologically as to effect the speed. The results are seen in tables 6 and 7.

Table 6 shows at 8:00 the maximum difference of speed of all the animals, between the two surfaces to be .16 mm. per second. At 2:00 the maximum difference is .1 mm. per second.

TABLE 6

Animal	time	Rock		Glass	
		no. of obs.	av. rate in mm. per sec.	no. of obs.	av. rate in mm. per sec.
2	8:30	8	1.15	7	1.21
3	until	7	0.98	7	0.92
4	11:00	9	1.17	7	1.01
2	2:00	7	0.99	9	0.99
3	until	7	1.02	9	1.12
4	4:00	7	1.01	5	1.11

Observations showing rate of locomotion. All the observations were taken on one day.

TABLE 7

Animal	time	Rock		Glass	
		no of obs.	av. rate in mm. per sec.	no. of obs.	av. rate in mm. per sec.
2	9:00	5	1.06	7	1.36
3	until	7	1.01	8	0.98
4	11:00	7	1.19	8	1.24
2	1:30	5	1.03	7	1.12
3	until	7	1.01	7	1.17
4	3:00	7	1.19	4	1.33

Observation showing rate of locomotion. All the observations were taken on one day.

Table 7, a day later, shows the maximum difference in rate at nine o'clock to be .3 mm. per second and at 1:30 o'clock to be .16 mm. per second. Further, in some cases the rate of speed is greater on the rock than on the glass.

The difference, then, in rate of locomotion between a smooth surface and a rough surface is so small as to be almost negligible. This further shows that the amount of slime extruded and secreted is not increased for a rough surface since this would probably reduce the speed of the animal.

According to Pearl, ('02), the method of locomotion in Planaria maculata is by means of the cilia beating in the mucus strands. Thinking that perhaps a study of the cilia and hypodermis might throw some light upon the thigmotaxis and locomotion of these animals, some work was done upon the histological structure of Phagocata gracilis.

Planarian tissue is one of the most difficult of animal tissues to study because it is so hard to fix properly and to stain. A fixative may give good results in one case and not in another. Five different fixing fluids were tried, hot Gilson's, hot and cold corrosive-acetic, twenty-five per cent solution of nitric acid, hot corrosive sublimate and a fixative recommended by Woodworth, ('91), made up of a saturated solution of corrosive sublimate in fifty percent nitric acid; of these, corrosive sublimate gave the best results. Of the various stains, borax-carmine, picrocarmine, neutral red, picric acid and carmine (aqueous), Delafields hematoxylin, Ehrlich's hematoxylin and eosin gave the best results. The sections were cut 6.6 microns thick. In all about thirty animals were studied.

The study was made principally of the hypodermis. On the ventral side, figure 2, it is made up of strongly ciliated columnar epithelial cells These contain large subcircular nuclei, nu, with evenly distributed chromatin granules. Definite cell walls between the cells could not be distinguished. Between the cells are spindle shaped, homogeneous bodies, the rhabditi, rb, which (Woodworth, '91) are developed in subcutaneous flask-shaped cells which are ectodermic in origin. These were supposed to be homologous to the nematocysts of the Coelenterata but later were supposed to be gland secretions. Underneath the hypodermis is a homogeneous layer, the basement membrane, bm. Under this is found the different muscle layers and the body parenchyma, figure 1.

The dorsal hypodermis, figure 3, is made up of columnar epithelial cells somewhat longer than those on the ventral surface. No cilia were found on these cells except near the edges of the animal. The rhabditi, rb, were much larger and more numerous than on the ventral hypodermis. They were found in groups of two or three. So thick were these that the nuclei of the cells, in many cases, were pressed out of shape and often concealed. The nuceli, nu, of the cells, when seen, appeared to have the same structure as those in the ventral side. Beneath the cell layer is found the basement membrane, bm. It is somewhat wider than on the ventral surface but has the same appearance. Beneath this membrane are the muscle layers and the parenchyma, mus. par. Imbedded in the parenchyma are numerous rhabditi mother cells, rb. mc, figure 1.

According to Woodworth, ('91) these rhabditi rapidly disintergrate when extruded into the water to form a slime which, by entangling the prey, aids the animal in procuring food. They may also be used for protection. Whether or not these rhabditi play any part in the locomotion of the animal, I was unable to determine.

In reviewing the literature on planaria there seems to be a difference of opinion among investigators regarding the distribution of cilia on the surface of the animal. Pearl ('02) finds none on the dorsal surface of Planaria maculata. Metschinikow ('66) and Kennel, ('79), found cilia covering the whole surface of Rhynchodesmus and Geodesmus but Zacharias, ('88), states that the dorsal surface of a variety of Goedesmus is bare. Vejdowsky, ('90), maintains the same for Microplana, the cilia in the latter cases being confined to the ventral surface or sole. Woodworth, ('91), found the cilia on Phagocata gracilis (collected near Cambridge, Mass.) to cover the entire surface of the body. I was able, tho I used the same technique as Woodworth, to find cilia only on the ventral surface and sides of the animal. However, these animals were collected in Falling Run, Morgantown, W. Va. This difference in localities may account for the variation in ciliation. Mosely, '74, explains that this absence of cilia on the dorsal surface of Bipalium may be due to the fact that the cilia on the dorsal surface of land planarians are weaker thru comparative lack of function and are more easily destroyed by reagents. However this is still an undecided question.

SUMMARY

The results in tables 1 and 2 show that there is a preference shown for a smooth surface rather than a rough one.

Tables 3 and 4, are interesting in that they substantiate the results found by Olmstead, ('17), that unfed Planaria maculata are positively geotropic, that is to say, have a tendency to keep the ventral side toward the stimulus of gravity. Likewise these results show that *Phagocata gracilis* is strongly negatively phototropic.

Since no mucus was found filling the grooves and cracks in the glass, it is clear that there must be no abnormal secretion of mucus and this is further strengthened by the results found in tables 5, 6 and 7, that there is an almost constant rate of locomotion on both a smooth and a rough surface. The last three tables also show that there is a variation in rate of locomotion which may be due to the different physiological states of the animal.

A histological study of the hypodermis discloses the fact that no cilia could be found on the dorsal side of the animal, which may be due to a difference in the variety of the variety of the animals, since Woodworth, ('91), found cilia on the dorsal hypodermis of the same species, collected in New England.

Conclusions

1. Phagocata gracilis is positively thigmotactic to a smooth surface.
2. This is not due to varying amounts of mucus secreted.
3. Phagocata gracilis is positively geotropic and strongly negatively phototropic.
4. The rate of locomotion is the same for both a rough and am sooth surface.
5. No cilia are found on the dorsal surface of Phagocata gracilis collected at Morgantown, W. Va.

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Morgantown, W. Va.

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Explanation of Plate

Plate XI

Fig. 1. Transverse section of the animal anterior to the mouth, × 22.
Fig. 2. Portion of the ventral hypodermis, × 2000, approximately.
Fig. 3 Portion of dorsal hypodermis, × 2000, approximately.

Lettering

bm.	basement membrane	*mus.*	muscle
cil.	cilia	*mus. par.*	muscle and parenchyma
c. mus.	circular muscle	*nu.*	nucleus
hyp.	hypodermis	*par.*	parenchyma
l. cil.	limit of cilia	*ph.*	pharynx
l. mus.	longitudinal muscle	*rb.*	rhabite
rb. mc.	rhabdite mother-cell		

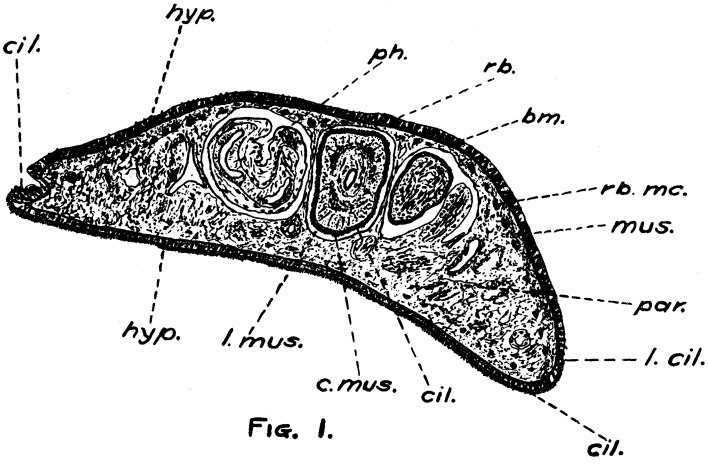

Fig. 1.

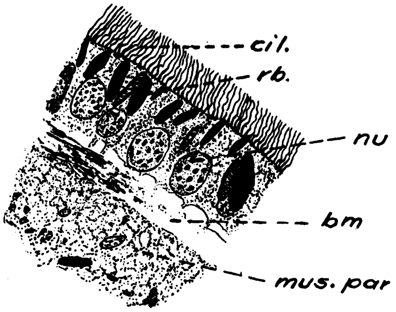

Fig. 2.

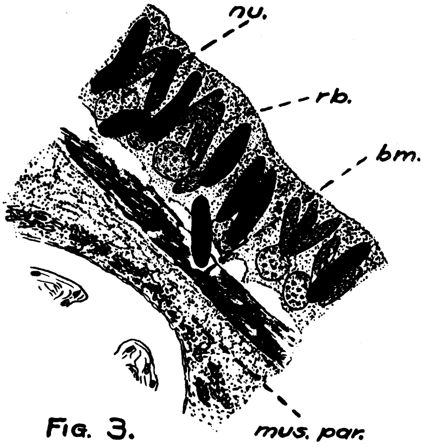

Fig. 3.

PLATE XI

WEIMER